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# Mammalian species abundance across a gradient of tropical land-use intensity: a hierarchical multi-species modelling approach

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## Abstract

Recent work in the tropics has advanced our understanding of the local impacts of land-use change on species richness. However, we still have a limited ability to make predictions about species abundances, especially in heterogeneous landscapes. Species abundances directly affect the functioning of an ecosystem and its conservation value. We applied a hierarchical model to camera- and live-trapping data from a region in Borneo, and estimated the relative abundance (controlling for imperfect detection) of 57 terrestrial mammal species, as a function of either categorical or continuous metrics of land-use change. We found that mean relative abundance increased (by 28%) from old-growth to logged forest, but declined substantially (by 47%) in oil palm plantations compared to forest. Abundance responses to above-ground live tree biomass (a continuous measure of local logging intensity) were negative overall, whilst they were strongly positive for landscape forest cover. From old-growth to logged forest, small mammals increased in their relative abundance proportionately much more than large mammals (169% compared to 13%). Similarly, omnivores and

insectivores increased more than other trophic guilds (carnivores, herbivores and frugivores). From forest to oil palm, species of high conservation concern fared especially poorly (declining by 84%). Invasive species relative abundance consistently increased along the gradient of land-use intensity. Changes in relative abundance across nine functional effects groups based on diet were minimal from old-growth to logged forest, but in oil palm only the vertebrate predation function was maintained. Our results show that, in the absence of hunting, even the most intensively logged forests can conserve the abundance and functional effects of mammals. Recent pledges made by companies to support the protection of High Carbon Stock logged forest could therefore yield substantial conservation benefits. Within oil palm, our results support the view that "wildlife-friendly" practices offer a low potential for reducing biodiversity impacts.

**Key words**: land-use change, abundance responses, selective logging, oil palm agriculture, High Carbon Stock, hierarchical modelling, robust monitoring, multi-method sampling, mammals, Borneo.

## 1. Introduction

Land-use change is well-known as a major driver of ecological change, for example as a leading cause of species endangerment at global scales (Vié, Hilton-Taylor & Stuart 2009). However, there remains a limited capacity to make biodiversity predictions, in particular of species abundances, at scales which are relevant to local stakeholders and policy-makers responsible for making land-use decisions. There are at least three reasons for this: 1) a focus on species richness rather than species abundances, 2) a failure to disentangle the observational and ecological processes than generate datasets, and 3) the characterisation of heterogeneous landscapes using categorical descriptors.

Much of the previous research on the biodiversity impacts of land-use change has focussed on community-level parameters, and especially species richness (Gibson *et al.* 2011). In this case, there is a developing consensus about the impacts of land-use change on species richness, such as the relatively lower impacts of selective logging relative to plantation forestry, which in turn often retain more species than monoculture plantations (Scales & Marsden 2008; Gibson *et al.* 2011; Barnes *et al.* 2014; Edwards *et al.* 2014). The more subtle impacts of land-use change on species abundances have been quantified less frequently, and often only for single focal species (e.g. from capture-recapture studies) or a limited subset of species (e.g. Berry *et al.* 2010). This matters because abundance estimates give a finer resolution of information on species responses to environmental change than species richness measures, and may therefore facilitate better decisions surrounding trade-offs in land-use (Phalan *et al.* 2011). Importantly, species abundances may also be indicative of ecosystem functioning (Ewers *et al.* 2015), as well as the trophic structure and interaction strengths present in an ecosystem (Barnes *et al.* 2014).

Across the studies in which abundance in tropical landscapes have been quantified, consistent patterns across land-use types, and across taxonomic groups, have remained elusive (Sodhi *et al.* 2009; Gibson *et al.* 2011; Newbold *et al.* 2014). The majority of past studies have based their inferences about abundance on sparse data, often on a small subset of species in a community, and without controlling for the potentially confounding set of observational processes which, in combination with the ecological processes at work, create observed datasets (Royle & Dorazio 2008). Perhaps most importantly, changes in detection probability across treatment units, such as different land-uses, may confound any apparent changes in abundance and must be controlled for (Archaux *et al.* 2011), something which has rarely been

done (e.g. see Newbold *et al.* 2014). The widespread failure to disentangle the observational and ecological processes at work may, at least in part, explain the large variability in reported abundance responses and, in the worst cases, may be a source of systematic bias in inferences. As a result, there is still a limited capacity to make robust predictions about the impacts of land-use change on species abundances (e.g. Newbold *et al.* 2014).

Land-use change sometimes involves dramatic and rapid changes to a natural habitat, for example when a primary forest is converted to pasture. More often, land-use in the tropics manifests itself as a gradient of disturbance intensity, rather than distinct land-use categories (e.g. Asner *et al.* 2009). For example, the intensity of selective logging may vary considerably across a landscape, due to access constraints and natural variability in marketable timber volumes (Berry *et al.* 2008). Similarly, plantations may vary in their proximity to remaining forests and in their structural properties, such as height and canopy cover, as they mature (Luskin & Potts 2011). Continuous, as opposed to categorical, metrics of land-use change are rarely used (Cushman *et al.* 2010), but may offer an opportunity to increase the predictive power and practical relevance of forecasts for conservation and management, especially in highly heterogeneous landscapes.

Land-use change has been especially acute in Southeast Asia, with the vast majority of remaining forest now existing in a logged-over state (Margono *et al.* 2014; Gaveau *et al.* 2014). Deforestation rates, in large part due to oil palm (*Elaeis guineensis*) plantation expansion, are also the highest among the major tropical forest regions (Asner *et al.* 2009). Palm oil producers, traders and buyers have increasingly recognised the reputational risk of being associated with deforestation, and dozens of the largest companies have recently made pledges to achieve "zero deforestation" within supply chains. In practice, the conservation of

High Carbon Stock (HCS) forest is likely to be the principal way these pledges will be implemented, with HCS forest delineated on the basis of gross structural properties (HCS Approach Steering Group 2015) or carbon-content (Raison *et al.* 2015). There is therefore an urgent need to consider the potential value of HCS forest for conserving biodiversity, and in particular the abundance of animal species.

Here we investigate species relative abundances for a community of terrestrial mammals across a land-use intensity gradient in Borneo. To do this, we use a hierarchical model of the mammal metacommunity in our study region which accounts for 1) changes in detection probability across space, 2) correlated detections in group-living species, 3) multiple sampling methods (camera traps and live traps), 4) a clustered sampling design, and 5) habitat filtering according to land-use and fine-scale habitat disturbance. We refer to "relative abundance", since our measure can be used to make robust comparisons across space (e.g. across land-use types), but not across species. We used either categorical or continuous approaches to characterise the land-use gradient. In the former case, we used three categories which match the major land-use options for a forested concession in the region: old-growth forest, logged forest and oil palm plantation. In the latter case, we used satellite-derived measures of above-ground live tree biomass (AGB) and local landscape percent forest cover. AGB is directly proportional to carbon content (Martin & Thomas 2011) and is therefore relevant for assessing the value of HCS set-aside areas for mammal species. Landscape forest cover is relevant to management decisions concerning the quantity of forest set-aside within a concession, for example as High Conservation Value (HCV) areas or riparian reserves in oil palm plantations (Koh, Levang & Ghazoul 2009). We also partitioned the mammal community according to four ecological response traits – body size, conservation status, native status and trophic guild – as well as into functional effects groups based on diet, and

present relative abundance and biomass responses of these sub-groups. For the first time, this allowed us to robustly explore whether particular sub-groups of Southeast Asian mammal species show differential responses to land-use change.

## 2. Materials and methods

### 2. 1. Sampling design

We sampled mammals across the landscape encompassed by the Stability of Altered Forest Ecosystems (SAFE) Project in Sabah, Malaysian Borneo (Ewers *et al.* 2011). This heterogeneous landscape consists of old-growth forest within the Maliau Basin Conservation Area and Brantian-Tatulit Virgin Jungle Reserve (VJR), repeatedly-logged forest within the Kalabakan Forest Reserve and two adjacent oil palm plantations straddling the Kalabakan Forest Reserve boundary (see Appendix S1 in Supporting Information for further description of the study sites).

We employed a clustered hierarchical sampling design, with 48 sampling points (23 m apart) clustered together into each of 46 sampling plots (each covering 1.75 ha), in turn clustered into 11 sampling blocks distributed across the land-use gradient (Fig. 1). This included 13 plots (in 4 blocks) in old-growth forest, 24 plots (in 4 blocks) in logged forest and 9 plots (in 3 blocks) in oil palm plantations. Sampling plots overlapped the SAFE Project sampling design, and therefore benefitted from the deliberate control of potentially confounding factors (including latitude, slope and elevation) that was central to this project's design (Ewers *et al.* 2011).

### 2. 2. Field methods

Of the 48 sampling points within each plot, a random subset of 13 points (range: 8 to 22) in each of the 46 plots were selected for camera-trapping, giving 590 points sampled in total. Camera-trapping methods followed Wearn *et al.* (2013), with cameras (Reconyx HC500, Holmen, Wisconsin, USA) deployed strictly within 5 m of each random point. Camera-trapping took place between May 2011 and April 2014, during which most plots (40 of 46) were sampled in multiple years (mean effort per plot = 635 trap nights). We excluded 18 points which had been camera-trapped for less than seven days, giving a total sampling effort of 29,121 camera trap nights (after correcting for camera failures).

Of the 46 plots sampled using camera traps, 31 were also sampled using live traps. Two locally-made steel-mesh traps (18 x 10 - 13 x 28 cm), baited with oil palm fruit, were placed at or near ground level (0 - 1.5 m) within 10 m (mean = 4.8 m) of all 48 points in a plot. Each trapping session consisted of seven consecutive trapping days and some plots (14 of 31) were sampled for multiple sessions across the study period (mean effort per plot = 1099 trap nights). Traps were checked each morning and captured individuals were anaesthetised using diethyl ether (following Wells et al. 2007), measured, permanently marked using a subcutaneous passive inductive transponder tag (Francis Scientific Instruments, Cambridge, UK), identified to species using Payne et al. (2007) and released at the capture location. Trapping, totalling 34,058 trap nights, was carried out between May 2011 and July 2014, during which there were no major mast-fruiting events (O. R. Wearn, pers. obs.).

We scored the habitat disturbance in a 5 m radius around each sampling point on a 1-5 scale, representing a scale of low to high disturbance intensity. For example, a score of 1 was used in intact, high canopy forest, whilst a score of 5 was used in open areas, such as on roads or

174 log-landing areas (full definitions are provided in Appendix S1). This variable was used to
175 model fine-scale variation in detection probability at the point scale.
176
177 2. 3. Modelling approach
178 To estimate species relative abundance, we used a form of multi-species occupancy model
179 (Royle & Dorazio 2008). These models all require replicate samples in space and time, in
180 order to separate the latent ecological processes of interest from the observational processes
181 by which the data are generated. We therefore transformed our data to the required form of
182 detections and non-detections within temporal replicates, or occasions, for each sampling
183 point. Here we define an occasion, for live-trapping, as a single night's trapping at a point
184 (i.e. two trap nights, given that two traps were deployed per point) or, for camera-trapping, as
185 five consecutive calendar days (see Appendix S1 for further information on camera trap data
186 pre-processing).
187
188 We here briefly describe the modelling approach we used (full details are provided in
189 Appendix S1), highlighting where it differs from related models in the literature (Yamaura *et*
190 *al.* 2011; Tobler *et al.* 2015). The observational process was characterised using the binomial
191 modelling approach of Royle & Nichols (2003), which uses the pattern of detections and non-
192 detections across sampling occasions (i.e. the detection history) to provide information on the
193 probability of detecting a species. Importantly, this model also exploits spatial heterogeneity
194 in this species-level detection probability to obtain a measure of relative abundance (local
195 abundance, as defined below), as well as the probability of detecting a single individual
196 animal (Royle & Dorazio 2008; Yamaura *et al.* 2011). We extended this approach to
197 incorporate multiple species and multiple sampling methods, by estimating individual-level
198 detection probability for each species-by-sampling method combination. For group-living

species, we used a quasi-binomial model for the observational process (estimating an additional overdispersion parameter in the process), to allow us to relax an assumption of independent detections among individuals (Royle & Dorazio 2008). We considered two point-specific covariates – land-use type and fine-scale habitat disturbance – acting on individual-level detection probabilities. We also included a $2^{nd}$-degree polynomial term for habitat disturbance, to allow for unimodal responses.

Local abundance ($\lambda$) – the latent ecological parameter in the model – was characterized by a zero-inflated Poisson mixed-effects model. Zero-inflation was incorporated at the land-use level, to allow species to be completely absent from certain land-use types, rather than just occurring at low abundance ($\lambda$ cannot be zero in a Poisson distribution). The local abundance estimates provided by the Royle & Nichols (2003) model represent, for a given species, the number of individuals using a given sampling point. In this study, we refer to this abundance measure as "relative abundance" rather than "true abundance" or density (individuals per unit area) because, although we have controlled for imperfect detection, this measure is not directly comparable across species. Local abundance will be a function of the effective trapping area for each species, as is also true of occupancy estimates (Efford & Dawson 2012). Specifically, we would expect a positive relationship between the home range of a species and its local abundance. However, local abundance likely serves as a robust measure of relative density changes across the land-use gradient, given that we controlled for detectability by land-use category and habitat disturbance. Our relative abundance measure is therefore spatially-comparable, and we restrict our inferences in this study to relative abundance comparisons across space, but not in absolute terms across species. Local abundance estimates are in units of individuals, irrespective of whether the species is group-living or not.

To account for our clustered sampling design, we used spatial random effects on local abundance, with sampling points nested within plots, in turn within blocks. In this study, we do not make inferences about the fine-scale variation in local abundance estimates. These estimates will be a function of both broad-scale population dynamics and local-scale use of habitat. We instead focus on the average local abundances (e.g. for a given land-use), having accounted for non-independence using the random effects. A temporal random effect of year enabled us to account for varying abundance across the multiple years of our study. Given this, we assume population and demographic closure over the time-scale of a year (i.e. that local populations do not go extinct or re-colonise, and that individuals are not dying, recruiting or migrating), but that changes can occur between years. However, by analogy with capture-recapture models, estimates may not be biased with a violation of closure, if changes in occupancy and local abundance are occurring at random (MacKenzie *et al.* 2006).

We characterised the land-use gradient in two different ways and present the relative abundance responses revealed by both approaches. The point-specific covariates on local abundance were either 1) categorical land-use types (abbreviated in the Results as LU) or 2) satellite-derived continuous metrics of AGB and percent forest cover (FCOV), both calculated within 500 m radius buffers around each sampling point (see Appendix S1 for further information). To allow for unimodal responses, we also included a $2^{nd}$-degree polynomial term for AGB. We did not include a polynomial term for percent forest cover because we had insufficient coverage of the covariate's full range within our sampled points, which meant that we did not have sufficient information to resolve any particular non-linear form of the response.

As in previous multi-species hierarchical models (Royle & Dorazio 2008; Tobler *et al.* 2015), species-level parameters in the observational and ecological components of the model were drawn from a common hyper-distribution for the metacommunity, rather than being modelled completely independently. This allows for inferences to be made about the most infrequently detected species by "borrowing strength" from the rest of the data, though this also involves making a trade-off for well-sampled species which could have been modelled independently (due to "shrinkage" of species-level parameter estimates towards the metacommunity mean). We made inferences from this model within a Bayesian framework, using JAGS (Just Another Gibbs Sampler) version 3.4.0 (Plummer 2013) to obtain samples of the joint posterior distribution (see Appendices S1-S2 for details of software implementation and model code). To test predictions about the overall effects (at the metacommunity level) of the categorical and continuous predictors on local abundance, we used the posterior distributions of the relevant hyperparameters to compute the probability that they were greater (or less) than zero.

To explore if particular mammal community sub-groups showed differential responses to land-use change, local abundance estimates for species were partitioned *post-hoc* according to ecological response traits: body size (large or small, using a 1 kg body mass threshold; 63% and 27% of species, respectively), conservation status (threatened or non-threatened on the IUCN Red List; 44% and 56% of species, respectively), native status (native or invasive; 95% and 5%, respectively) and trophic guild (carnivore, insectivore, frugivore, herbivore or omnivore; 21%, 21%, 28%, 9% and 21% of species, respectively). We also defined nine functional effects groups based on diet, i.e. all species implicated in each of: vertebrate predation, scavenging, invertebrate predation, fruit-eating, seed-eating, fungi-eating, leaf-eating, bark-eating and root-eating (see Appendix S1 for more information). Local biomasses

(the biomass of individuals using a given sampling point) were calculated by multiplying local abundance estimates by body mass estimates for each species. As for abundance, our measure of biomass is a spatially-comparable "relative biomass" measure, rather than biomass density (biomass per unit area).

## 3. Results

A total of 4,381 live trap captures and 15,148 camera trap captures were made, for 57 mammal species. After reducing these data into detections or non-detections within sampling occasions (17,025 live trap occasions and 5,428 camera trap occasions), this translated into 4,284 live trap detections of 23 species, and 7,772 camera trap detections of 53 species (19 species were common to both sampling methods). We also had a limited number of captures (mostly $\leq 2$ per species) for nine additional mammal species which we classified as obligate arboreal species (listed in Appendix S1) and which we did not include in our abundance models.

### 3. 1. Relative abundance responses to land-use type

Mean local abundance across the mammal community was marginally higher (+28%, CI: -5 to 66%) in logged forest compared to old-growth forest ($\Pr(\beta^{\lambda,LU}_{Logged} > 0) = 0.76$), but much lower (-47%, CI: -67 to 8%) in oil palm compared to the two forest land-uses ($\Pr(\beta^{\lambda,LU}_{OilPalm} < 0) = 1.00$). These overall trends, however, belie substantial differences among species groups (Fig. 2) and among individual species (Fig. 3; Appendix S3).

From old-growth to logged forest, large mammals exhibited a modest (+13%, CI: -18 to 51%) increase in mean local abundance, but small mammals increased substantially (+169%, CI: 67 to 292%). The mean local abundance of high conservation concern species was similar in

logged forest compared to old-growth forest (Fig. 2), but dropped precipitously (-84%, CI: -93 to -59%) in oil palm compared to the two forest land-uses. In contrast, the local abundance of low conservation concern species was largely robust to the land-use gradient, whilst invasive species increased substantially along the gradient of land-use intensity (Fig. 2). There was a 27% chance of invasive species (one or more species) being present in old-growth forest (none were detected during sampling). From logged forest to oil palm, the local abundance of invasives increased by 598% (CI: -19 to 5644%). The mean local abundance of all trophic guilds except frugivores increased from old-growth to logged forest, whilst the local abundance of all guilds except carnivores declined in oil palm (Fig. 2).

The trends in summed local abundances and biomasses (i.e. summed across species) for each trait-defined group were largely similar to those for mean local abundance (Appendix S3). However, the relatively modest local abundance increases in herbivores (+14%, CI: -36 to 112%) and threatened species (+29%, CI: -10 to 83%) from old-growth to logged forest were much more prominent in terms of summed local biomass (113% and 99%, respectively), due to increases in large-bodied species in these groups (e.g. sambar deer *Rusa unicolor*, banteng *Bos javanicus* and Asian elephant *Elephas maximus*). Similarly, large changes in mean local abundance in omnivores (97%, CI: 24 to 211%) were not as strong in terms of summed local biomass (49%, CI: -17 to 174%), because these abundance changes were partly driven by small-bodied murid rodent species.

The summed local biomasses of functional effects groups were maintained, or increased, from old-growth to logged forest, but from forest to oil palm substantial declines were evident in all cases except vertebrate predation (Fig. 4).

3. 2. Relative abundance responses to continuous metrics of land-use intensity

Local abundance was negatively affected overall by AGB ($\Pr(\beta^{\lambda,AGB} < 0) = 0.96$) and positively affected by forest cover ($\Pr(\beta^{\lambda,FCOV} > 0) = 1.00$; Figs. 5-6). The effect of forest cover was stronger than the effect of AGB (standardised hyperparameter estimates: $\beta^{\lambda,AGB} = -0.18$, CI: -0.35 to -0.01; $\beta^{\lambda,AGB^2} = -0.10$, CI: -0.22 to -0.003; $\beta^{\lambda,FCOV} = 0.68$, CI: 0.38 to 0.98), and this was also true at the species level in most cases (Appendix S3). There was evidence of overall unimodal responses to AGB ($\Pr(\beta^{\lambda,AGB^2} < 0) = 0.96$), albeit with a weak effect (as confirmed visually), and this was also generally the case for individual species. Some species (e.g. long-tailed giant rat *Leopoldamys sabanus*, Low's squirrel *Sundasciurus lowii*, plain treeshrew *Tupaia longipes* and sambar deer) exhibited stronger threshold responses, in which increases in abundance with decreasing AGB were not maintained below ~ 90 Mg/ha (Appendix S3).

All ecological response trait groups except frugivores showed a negative relationship between local abundance and AGB (Fig. 5A). The relationships were most strongly negative in omnivores, small mammals and invasives (Fig. 5A), all groups which are dominated by murid rodent species. All ecological response trait groups except carnivores and invasives showed a positive relationship between local abundance and forest cover (Fig. 6A). Mean carnivore local abundance exhibited a unimodal response curve, being lowest at ~ 70% forest cover (Fig. 6A). This reflects a shift from native forest-dependent predators, including the yellow-throated marten (*Martes flavigula*) and Sunda clouded leopard (*Neofelis diardi*), to native and non-native carnivores tolerant of more open habitats, principally the leopard cat (*Prionailurus bengalensis*), Malay civet (*Viverra tangalunga*) and domestic dog (*Canis familiaris*). For the continuous metrics, we also calculated the mean across species of the

348 percentage change in local abundance along the land-use gradient (effectively giving each
349 species equal weight, irrespective of their absolute abundance). This measure exhibited
350 similar trends to the mean local abundance of each species group (Figs. 5B and 6B), except
351 there was stronger evidence in some groups of lower rates of abundance increases, or even
352 decreases in abundance, at lower values of AGB (< 90 Mg/ha), and there was no evidence of
353 a recovery in carnivore local abundance at low forest cover. These slight differences arise
354 because patterns in mean local abundance are determined primarily by abundance shifts in
355 species with the highest local abundances.
356
357 The summed local biomasses of the dietary functional effects groups were mostly negatively
358 affected by AGB and, except in the case of vertebrate predation, were positively affected by
359 forest cover (Appendix S3).
360
361 **4. Discussion**
362 Mammalian relative abundance (controlled for imperfect detection) was conserved, or
363 increased, from old-growth to logged forest overall, whilst it declined substantially from
364 forest to oil palm plantations. This was true of mean and summed local abundance, as well as
365 local biomass. Mammalian relative abundance (mean and summed) and biomass responses to
366 decreases in local landscape AGB due to logging were positive, albeit weakly unimodal, but
367 were strongly negative for decreases in local landscape forest cover. It was primarily losses in
368 forest cover, and not forest degradation, that negatively affected the conservation value of
369 local landscapes in our study region.
370
371 Few previous studies in the region have investigated abundance responses to land-use
372 change, but apparent trends across various taxonomic groups (based on uncorrected

abundance measures) have usually been similar to our results. Abundance in logged areas has usually been found to be maintained at a community level (Wells *et al.* 2007; Slade, Mann & Lewis 2011; Edwards *et al.* 2011), but substantially declines in oil palm plantations (e.g. Turner & Foster 2008; Edwards *et al.* 2010). However, our study is the first time, to our knowledge, that a robust assessment of animal relative abundance has been made along the principal land-use gradient in Southeast Asia.

4. 1. The conservation value of heavily-degraded forests

The evidence overall, taken together with our findings for mammals, increasingly supports the view that large, contiguous areas of logged forest in Southeast Asia not only conserve similar levels of species richness to old-growth forest (e.g. Edwards et al., 2014), but also conserve the community-level abundance of many groups. We note that this was true in our study even in the absence of any significant spill-over effect from large, continuous areas of old-growth forest (which were > 20 km away from our logged forest sites). This adds further emphasis to the calls for increasing recognition of logged forest as an essential part of the conservation estate (Edwards *et al.* 2011). These degraded forests have been the primary source of new land for expanding plantations in the region (Margono *et al.* 2014), but could represent a relatively low opportunity-cost option for conservation, given that much of their timber value has been extracted (Edwards *et al.* 2014). Our study is also one of the few that has been undertaken in repeatedly-logged forests (Edwards *et al.* 2011, 2014; Woodcock *et al.* 2011; Struebig *et al.* 2013), and the finding that terrestrial mammal community richness and abundance is maintained even in these heavily-degraded forests further strengthens the argument for low-cost conservation in such areas. There are signs that this argument is gaining traction in the Malaysian state of Sabah, at least, with the government recently setting-aside > 3,000 $km^2$ of logged forest for conservation (Reynolds 2012).

The biggest caveat on the conservation value of heavily-degraded forest is that hunting is strictly controlled. Bushmeat hunting is widely-practiced in logged-over forests (Bennett & Gumal 2001), and can lead to local population extirpations of high-value mammal species (Harrison *et al.* 2016). Brodie *et al.* (2015) found that the effect of hunting on large mammal occupancy was stronger than that of logging for most of the species investigated. Hunting pressure was very low across our study sites, due to inaccessibility and cultural factors (Appendix S1).

4. 2. A trait-based view of mammal communities under land-use change

By assessing the whole terrestrial mammal community, we were also able to go further than previous studies in the region and assess the relative abundance responses of important sub-groups of mammals defined by their traits, as well as the potential functional effects of changes in relative abundance across the community. We found that, for almost all response trait groups, logged forests retained similar or higher local abundances (mean and summed across species) and biomasses compared to old-growth forest. This was also true for the local biomasses of functional effects groups we examined, a finding which is consistent with other evidence that the functional role of vertebrates increases in logged relative to old-growth forests (Ewers *et al.* 2015). Moreover, these group-level increases were largely maintained even at very low levels of AGB in a local landscape, indicative of high levels of logging disturbance. On the other hand, our results indicate that conversion to oil palm, and reductions in forest cover, cause declines in the local abundance (mean and summed) and biomass of almost all the trait-defined sub-groups we examined (not carnivores and invasives), as well as in the local biomasses of almost all the functional effects groups (not vertebrate predation).

Across the mammal sub-groups we assessed, small mammals exhibited the most dramatic change in relative abundance (in terms of both mean and summed local abundance), increasing substantially in logged forest, and also in response to declining AGB, similar to findings elsewhere in tropical forests (Isabirye-Basuta & Kasenene 1987; Lambert, Malcolm & Zimmerman 2006). This may have important implications for plant recruitment, since small mammals are significant seed predators in these forests (Wells & Bagchi 2005). For large mammals, the changes in relative abundance were not as dramatic as for small mammals, though we note that in this case the change in local biomass was much greater than the modest change in mean local abundance suggested. Much of this increase in local biomass was driven by a shift towards herbivore species with a larger body size. An increase in herbivore biomass will likely have as strong effects on ecosystem functioning as an increase in the abundance of small mammal seed predators, through changes in seedling recruitment rates (Harrison *et al.* 2013) and nutrient cycling (Wardle & Bardgett 2004).

Across the trophic guilds, we found that omnivores increased markedly in logged compared to old-growth forest, perhaps because wide dietary breadth confers dietary flexibility. This is likely the case for most of the omnivorous species in our dataset, including the murid rodents, bearded pig (*Sus barbatus*) and sun bear (*Helarctos malayanus*).

For insectivores, some studies on birds have shown a disproportionate sensitivity to disturbance for this guild (Gray *et al.* 2007). We found that mammalian insectivores increased in logged compared to old-growth forest. The abundance responses of insects, and invertebrates more generally, to logging is poorly known in Southeast Asia, but we note that, at our study sites, invertebrate biomass is apparently higher in logged forest compared to old-

448 growth forest (Ewers *et al.* 2015), potentially indicating that food resources for insectivorous
449 mammals are higher.
450
451 For carnivores, the increase from old-growth to logged forest we observed would be expected
452 based on a numerical response to the increased abundance of vertebrate prey. Most of the
453 carnivores we studied, and in particular the felids, focus on mammal prey such as murid
454 rodents (Grassman *et al.* 2005).
455
456 Frugivory is a trait which has often been associated with an increased susceptibility to
457 disturbance (Gray *et al.* 2007), but it is not clear whether logging consistently causes a
458 decline in fruit availability or not (e.g. Wong, 1986; Heydon & Bulloh, 1997; Munshi-South
459 et al., 2007). Certainly, some key fruiting resources such as hemi-epiphytic figs are often
460 much reduced after logging (Lambert 1991), but the availability of small fruit on lianas and
461 understorey shrubs might increase in gaps or along edges (Davies *et al.* 2001). Frugivores
462 exhibited no change in relative abundance from old-growth to logged forest, but modelling
463 using the continuous AGB metric revealed a modest decline in relative abundance with
464 increasing logging disturbance. We note, however, that the summed local biomass of all
465 species engaging in fruit-eating did not decline, suggesting frugivory as a function may be
466 resilient to logging, even though specialist frugivores do not fare as well as other groups.
467
468 Finally, of crucial conservation relevance, we found that the relative abundance of high
469 conservation concern species was retained in logged forests, and that this group was resilient
470 even to high intensities of logging (low levels of AGB) in a given local landscape. We should
471 emphasise, however, that this does not necessarily mean that high conservation concern
472 species would persist in hypothetical landscapes consisting of homogeneously low AGB

areas; AGB values refer to an average over a local landscape, and will contain some patches of less intensively logged forest, as well as areas that are heavily-disturbed.

### 4. 3. The promise of High Carbon Stock forest for conservation

Recent "zero deforestation" pledges within the palm oil industry represent an important positive step towards the increased conservation of heavily-disturbed forests. Removing deforestation from supply chains will, in practice, require a consistent definition of what constitutes a forest, and current dialogue has so far focussed on a carbon-based definition, in particular a threshold of ≥ 35-50 MgC/ha to define HCS forest (HCS Approach Steering Group 2015; Raison *et al.* 2015). This is equivalent to an AGB of ~ 75-100 Mg/ha (assuming that carbon constitutes 47% of live tree biomass; Martin & Thomas, 2011), which could, if our findings apply more broadly in the region, yield major conservation benefits for mammals over the business-as-usual. Indeed, none of the mammal sub-groups we assessed, apart from frugivores, showed evidence of substantial relative abundance declines in forest with low AGB, suggesting that an even lower threshold for delimiting HCS could yield even larger conservation benefits. We emphasise, however, that the conservation potential of HCS forests for mammals will only be realized with additional investment to manage hunting pressure.

An important uncertainty remains surrounding the patch size at which HCS forest will be delimited in practice. We modelled relative abundance responses to AGB within 500 m buffers, but clearly this patch size is insufficient to maintain viable mammal populations. The conservation value of HCS forest set-aside will also lie in its spatial extent and connectivity, not just in the intensity of local logging disturbance.

498 4. 4. Mammal conservation in oil palm landscapes

499 Our conclusions concerning the conservation potential of oil palm are less optimistic.
500 Although the plantations in which we sampled may represent something of a best-case
501 scenario for oil palm, with relatively high levels of landscape forest cover and relatively low
502 levels of hunting, our modelling of mammal relative abundance as a function of forest cover
503 indicates only a very limited potential for conservation gains by attempting a land-sharing,
504 'wildlife-friendly' approach (e.g. Koh, Levang & Ghazoul 2009) to this land-use. Increases in
505 local landscape forest cover from 0 to 30%, the likely range which could realistically be
506 manipulated in oil palm landscapes, resulted in very limited relative abundance increases
507 across species groups and across most individual species within the oil palm crop, suggesting
508 only a limited degree of spill-over from remnant forest patches. Among trophic guilds, only
509 carnivores showed some resilience to decreases in forest cover, but this was in large part
510 driven by increases in free-ranging domestic dogs, which are considered a detrimental
511 invasive species across Asian landscapes (Hughes & Macdonald 2013). We did not sample
512 remnant forest fragments within the oil palm, but it is unlikely that the abundance and
513 richness of mammals in these areas would approach that of contiguous forest (Bernard *et al.*
514 2014), even if individuals present in the oil palm crop itself were also counted. Overall, this
515 indicates that a land-sparing approach might better serve mammal conservation in the region,
516 in which companies are encouraged to invest in the off-site conservation of large, contiguous
517 forest areas (Edwards *et al.* 2010), rather than attempting to increase mammal populations
518 within their plantations by retaining small forest patches. As a caveat to this, there may be the
519 potential for 'win-win' solutions for both conservation and oil palm yield, such as in the bio-
520 control of pest species, and in this case on-site conservation activities should be encouraged
521 (Foster *et al.* 2011). In particular, the high relative abundance of leopard cats we found within

522 the oil palm crop, and the low relative abundance of invasive murid rodents, suggests a
523 possible role for this species in bio-control.
524
525 4. 5. Conclusions
526 Across a large assemblage of Southeast Asian mammal species, we have shed light on the
527 contrasting relative abundance responses to logging and conversion to oil palm. We have also
528 uncovered the relative abundance responses to the continuous metrics of logging intensity
529 and forest cover loss. These results have direct relevance for conservation and management at
530 local scales. Specifically, they suggest that conservation efforts should be directed at
531 safeguarding all remaining forest in the region, both old-growth and logged forests alike, and
532 that multiple-use landscapes (consisting of oil palm and small forest patches) will not be
533 effective for conservation.
534
535 The hierarchical modelling approach that we used, which can integrate data from multiple
536 sources, could be applied to other taxonomic groups and other land-use types. This could
537 pave the way for more robust biodiversity forecasting and more effective decision-making in
538 the face of biodiversity trade-offs across land-use.
539
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## Supporting Information

**Appendix S1.** Supplementary methods.

**Appendix S2.** Model code in BUGS (Bayesian inference Using Gibbs Sampling) language.

**Appendix S3.** Supplementary results.

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724

## Figures

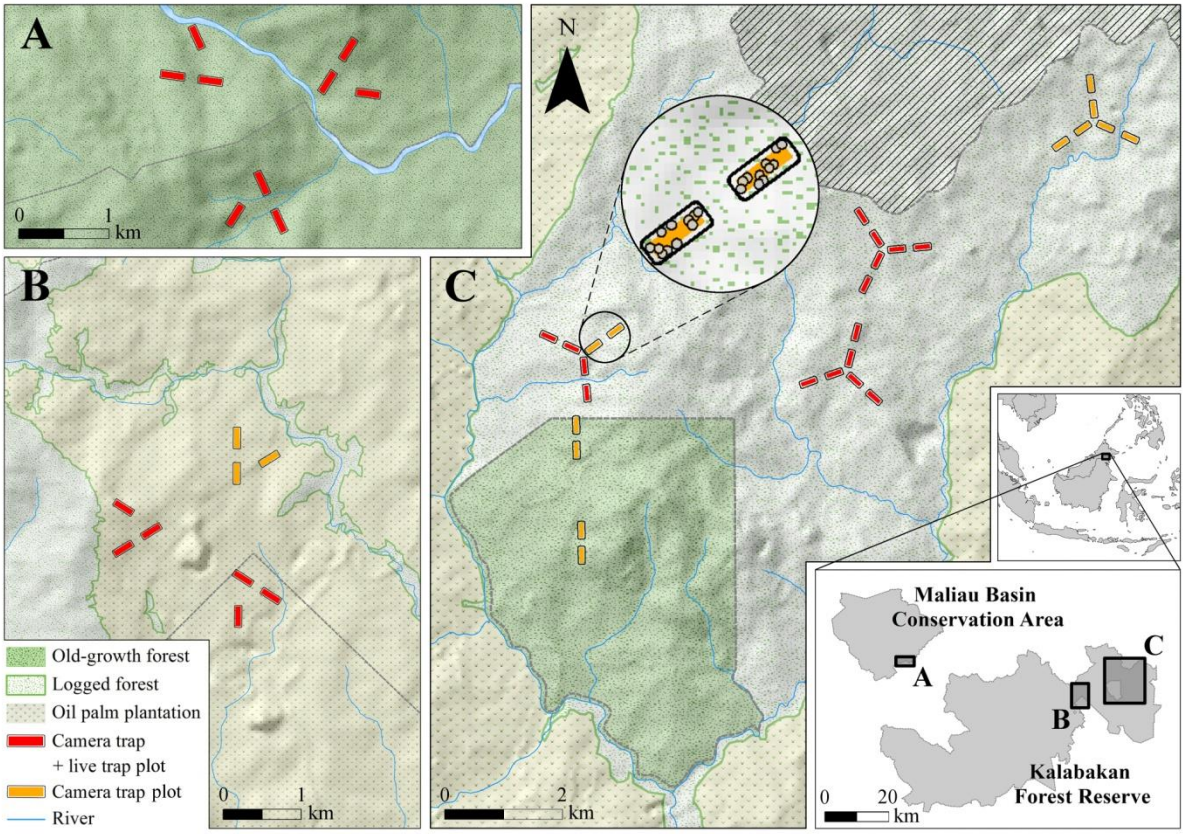



**Fig. 1**. Sampling design across a gradient of land-use intensities in Borneo, showing the plots sampled using both camera traps and live traps (in red) and plots sampled only with camera traps (in orange). The Kalabakan Forest Reserve connects to an extensive (>1 million ha) area of contiguous logged forest to the north (hatched area). Insets show: an example of how cameras were arranged within plots; the location of the study within insular Southeast Asia, and the spatial proximity of panels A to C within south-east Sabah, Malaysia. Land-cover surrounding the Maliau Basin and Kalabakan Forest Reserve (white areas in the inset map) was a mosaic of logged forest and plantations.

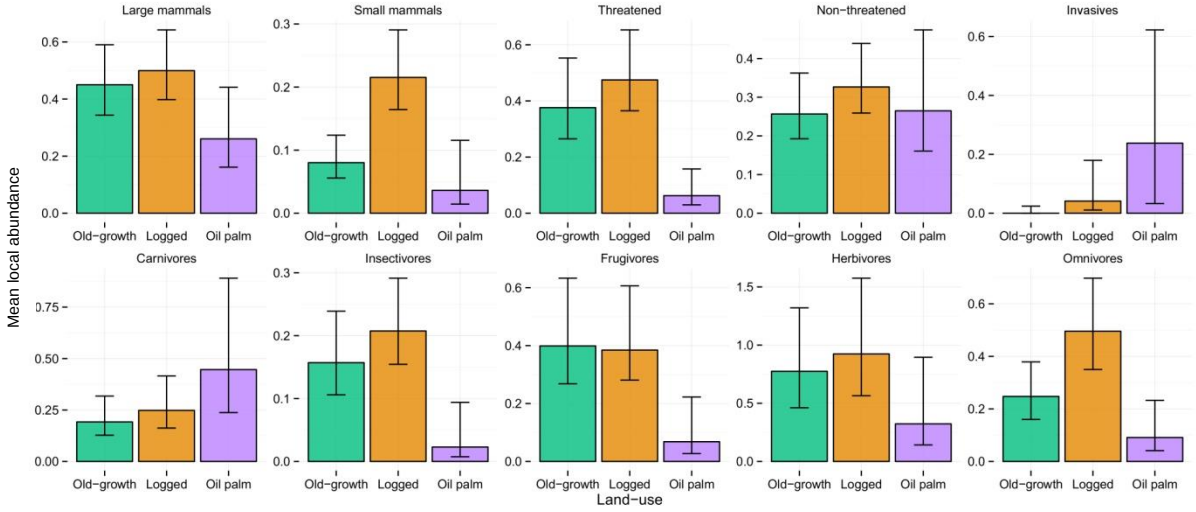



**Fig. 2**. Local abundance of mammals (average across species) across land-use categories, partitioned by ecological response groups defined by body size (large and small mammals), conservation status (threatened, non-threatened), native status (only invasives shown) and trophic guild (five mutually-exclusive feeding guilds). Error bars indicate 90% credible intervals.

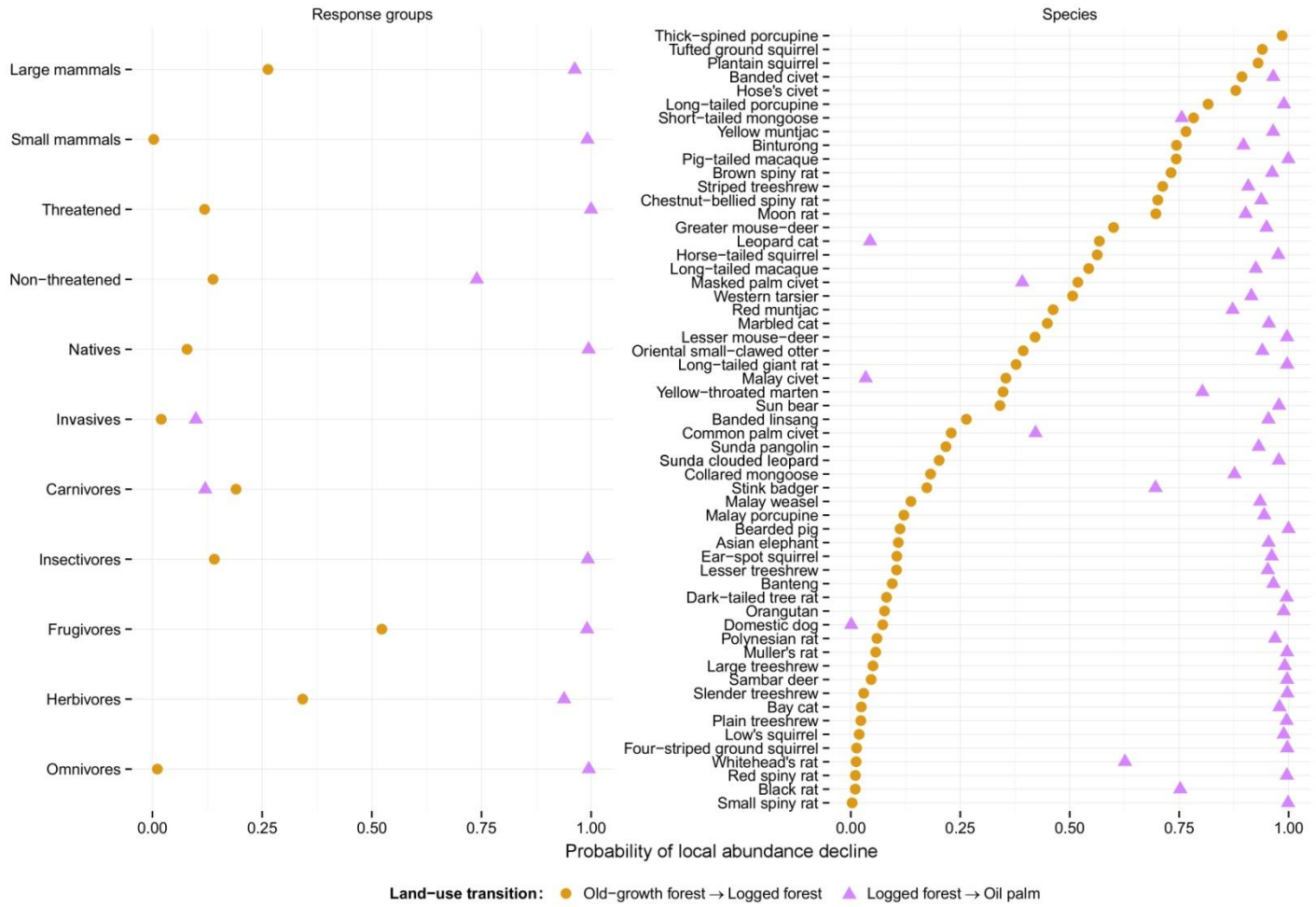
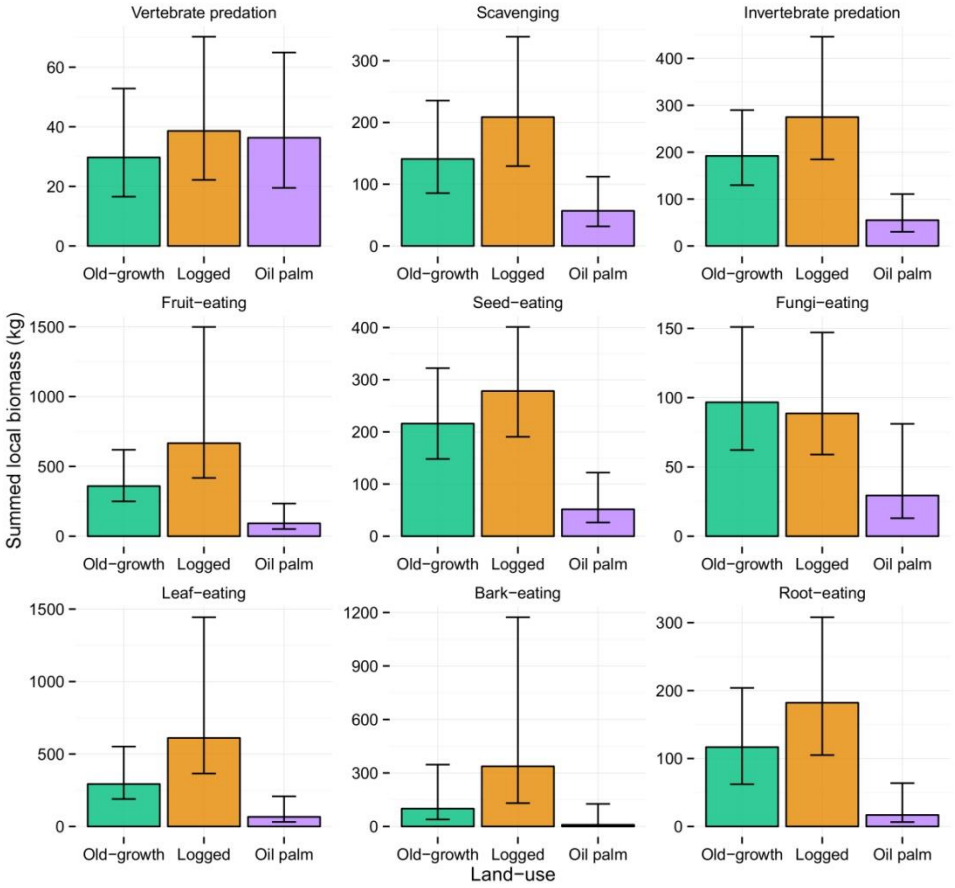



**Fig. 3**. Probabilities of a decline in local abundance from old-growth to logged forest (orange) and from logged forest to oil palm (purple), for each ecological response group and each mammal species. We did not calculate the probability of decline from logged forest to oil palm for four species which were not recorded in logged forest.




746

747 **Fig. 4**. Summed local biomass of mammals (a relative biomass measure) across land-use

748 categories, partitioned by functional effects groups based on diet. Error bars indicate 90%

749 credible intervals.

750

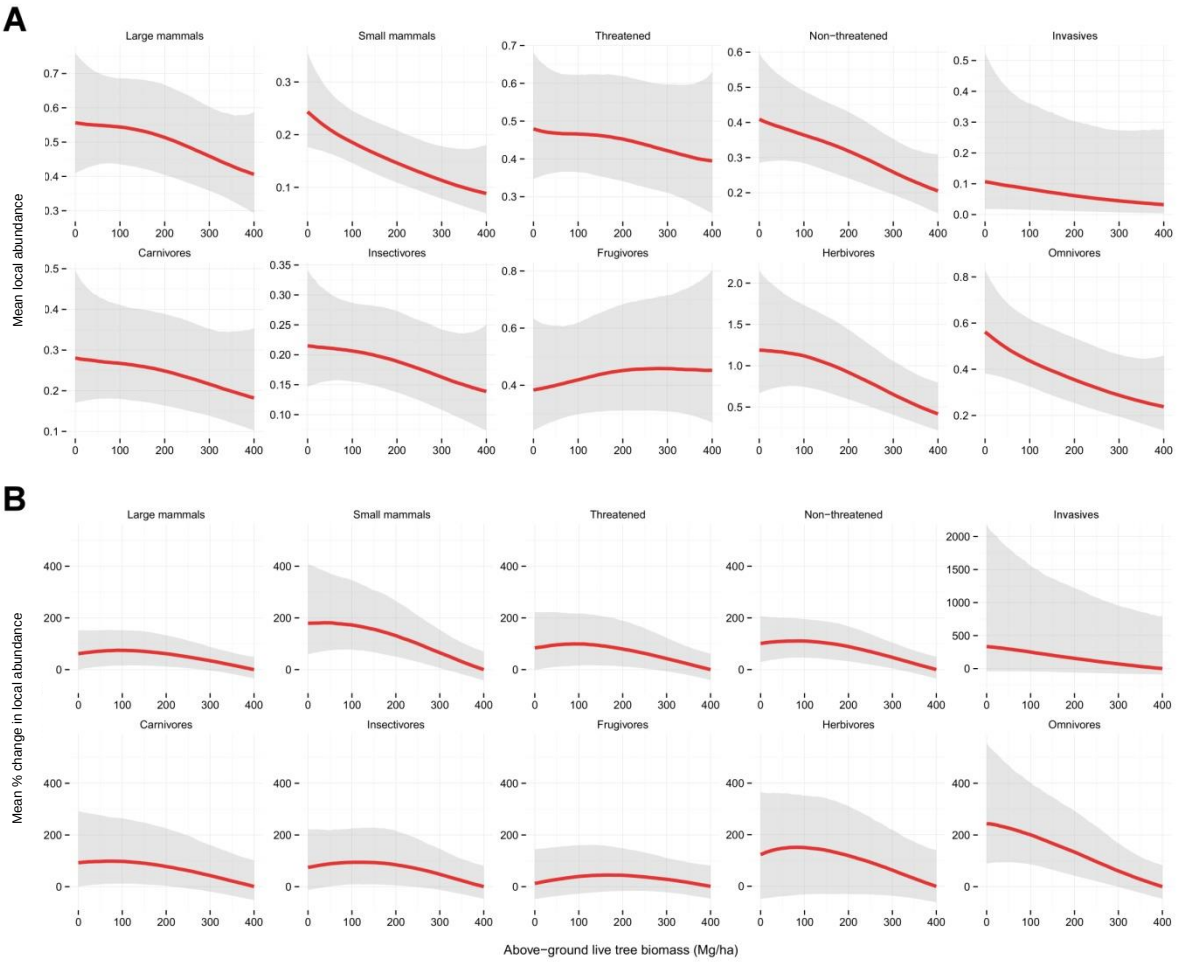
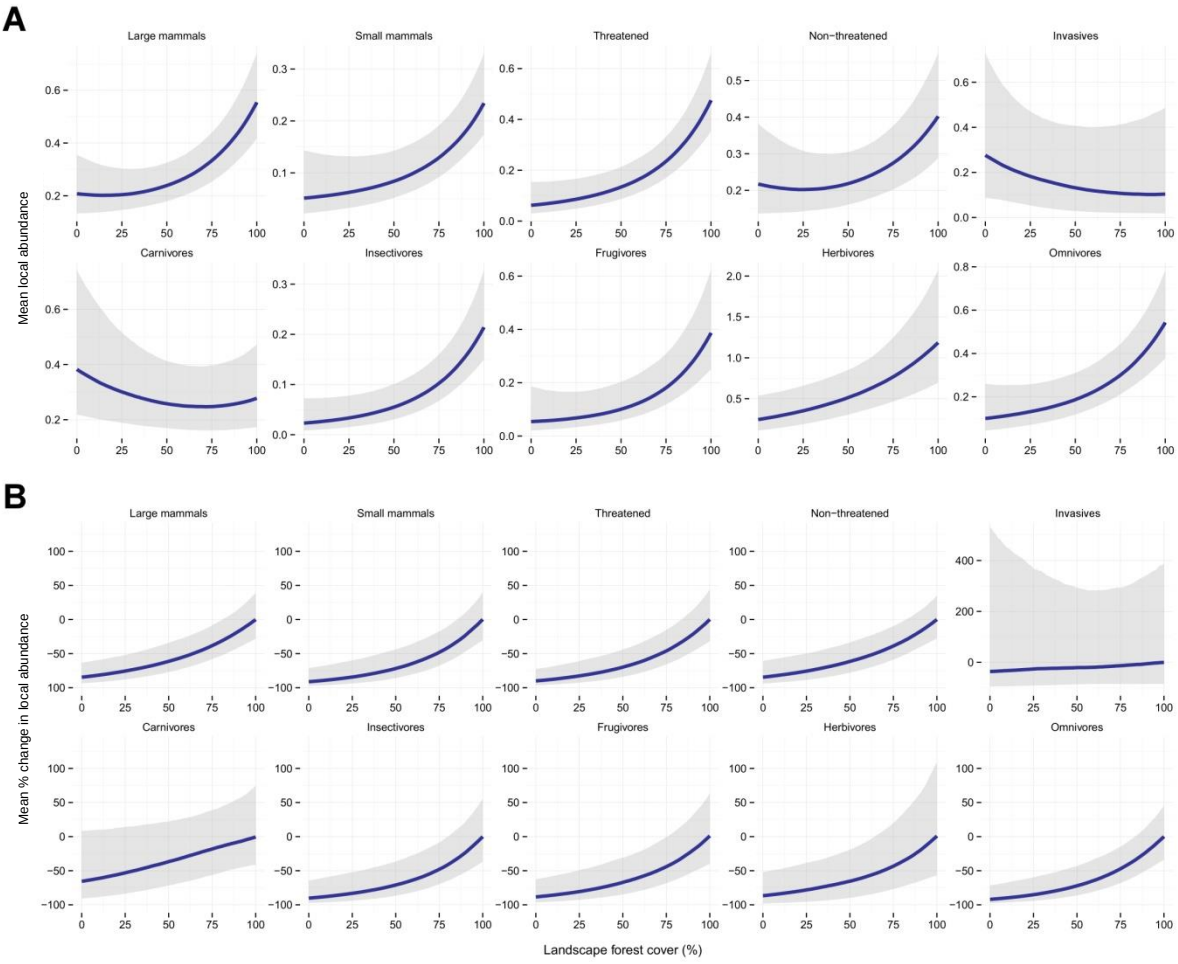



**Fig. 5**. Local abundance (A) and percentage change in local abundance (B) averaged across mammal species, as a function of above-ground live tree biomass in a given local landscape. Species are partitioned by ecological response groups defined by body size, conservation status, native status (only invasives shown) and trophic guild. Percentage change refers to the change relative to the abundance at AGB values typical of intact forest (400 Mg/ha). Forest cover was fixed at 100%. 90% credible intervals (in grey) indicate uncertainty surrounding median estimates (red line).




760

761 **Fig. 6**. Local abundance (A) and percentage change in local abundance (B) averaged across
762 mammal species, as a function of forest cover in a given local landscape. Species are
763 partitioned by ecological response groups defined by body size, conservation status, native
764 status (only invasives shown) and trophic guild. Percentage change refers to the change in
765 abundance as forest cover decreases from 100%. Above-ground live tree biomass was fixed
766 at the average across oil palm locations. 90% credible intervals (in grey) indicate uncertainty
767 surrounding median estimates (red line).

768

769